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THE UNIVERSITY OF ALBERTA

POST-DAM VEGETATION CHANGES AND SMALL MAMMAL POPULATIONS IN THE PEACE-ATHABASCA DELTA

by

Olivier Pfister

(C)

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS OF THE DEGREE OF M.Sc.

IN

WILDLAND RECREATION

DEPARTMENT OF FOREST SCIENCE

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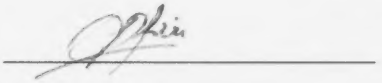

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October 8, 1993

Abstract

This research was undertaken to estimate the impact of the invasion of grass meadows by willows on small cricetinid and zapodid rodent populations in the Peace-Athabasca Delta of Wood Buffalo National Park. Live trapping grids covering an area of 0.74 hectare were established on adjacent grass meadow and willow vegetation types in three study sites. Population estimates were obtained by the minimum number known alive method and were used to calculate biomass of small mammals in grass meadow and willow grids.

Mean trapping estimates of adult meadow voles *(Microtus pennsylvanicus)* ranged from less than 1 individual per hectare on the willow grids to 28 individuals per hectare on the meadow grids. Mean trapping estimates of 6 individuals per hectare were obtained for adult populations of deer mice *(Peromyscus maniculatus)* and red-backed voles *(Clethrionomys gapperi)* on the willow grids while populations of adult meadow jumping mice *(Zapus hudsonius)* only reached a mean of less than 1 individual per hectare. These three species were absent from the meadow grids. Total biomass of the above species ranged from 275 gram/hectare on the willow grids to 1093 gram/hectare on the meadow grids.

The pattern of habitat preference per species between willow and meadow grids in each of the three study sites was statistically significant ($P<0.05$).

It is estimated that the development of grass meadows into willow shrublands vegetation type in the next two to four decades could result in a loss of more than 50% of the biomass of small cricetinid and zapodid rodents that was present in those meadows in 1976. This decrease in biomass should have a negative affect on the foraging efficiency and producitivity of secondary consumers (although trapping records of the last 40 years did not yet reveal any significant correlation between the trapping returns of weasel and

ermine pelts -*Mustela* spp.- and the construction of the Bennett Dam). Other predators that might be affected include: fisher (*Martes pennanti*), marten (*Martes americana*), merlin (*Falco columbarius*), American kestrel (*Falco sparverius*), northern harrier (*Cirus cyaneus*) and short-eared owl (*Asio flammeus*).

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Introduction

Despite massive hydro-electric developments in northern Canada, relatively few studies regarding the ecological impact of dams on the environment have been completed. To mitigate potential negative repercussions of future dam projects in the North, more baseline information is needed on the resulting perturbations from such projects that affect ecosystems. Research aimed at monitoring wildlife populations is a useful way to estimate the impact and consequences of hydro-electric projects on northern deltas. On a more global basis, such studies could give valuable insights on the potential effect of the drying of deltas in the context of global climate change.

The Peace-Athabasca Delta represents a unique site to study such effects. The Delta, which is located within Wood Buffalo National Park, is one of the most extensive northern inland deltas in the western hemisphere (Peace-Athabasca Delta Group, 1972). However, the construction of the W.A.C. Bennett Dam in 1968 has had serious repercussions on its ecological integrity (Peace-Athabasca Delta Group, 1973;Peace-Athabasca Delta Implimentation Committee, 1987). The resulting lower water levels and colonization of grass meadow communities by willows and the movement of shoreline has affected wildlife distribution and population levels.

Most of the post-dam wildlife studies done in the Delta have, until now, dealt with waterfowl, bison and muskrat (Peace-Athabasca Delta Group, 1972;Westworth, 1974). However, the effect of the vegetation changes should be particularly noticeable among small mammals since most of them are strong habitat selectors (M'Closkey, 1975;M'Closkey and Fieldwick, 1975;Morris, 1983) and population turnover is high as compared to that of other mammals. These characteristics make them ideal study subjects since they will be among the first mammals to be affected. Furthermore, since small mammal populations occupy a relatively low position on the food chain, the

repercussions of the vegetation changes on the higher predators in the ecosystem will, in part, depend on the variations in small mammal biomass.

Results of previous studies conducted in other geographical locations have schown that the four species of small mammals studied in this research are often found in specific habitats.

In the boreal zone, deer mice (*Peromyscys maniculatus*) are usually present in forests adjacent to meadows (Galindo, 1984). Factors often associated with microhabitat of deer mice are: shrub and low vegetation cover which seem to be positively correlated with the presence of deer mice (Crowell and Pimm, 1976;Van Horne, 1982;Vickery *et al*, 1989), and a dense vertical cover (Wywialowski, 1987). In fact, when forced to choose between the two types of covers, deer mice seem to select vertical cover over horizontal cover (Wywialowski, 1987). Dueser and Porter (1986) and Merkt (1981) when conducting trapping in forests, shrublands, grasslands and salt marshes, reported the highest density of deer mice in shrublands.

Red-backed voles (*Clethrionomys gapperi*) , on the other hand, seem to prefer mature forests (Halvorson, 1982;Martell, 1983;Ovaska and Herman, 1986) although they also have been observed in woody and bushy *(Salix, Alnus, Betula)* riparian habitats (Millar *et al*, 1985), including willow-covered levees (Wrigley, 1974). Main characteristics of red-backed vole microhabitat include dense ground cover (Lovejoy, 1975;Martell and Radvanyi, 1977) and the availability of mushrooms (fungi) and, to a lesser extent, berries, both of which constitute important food items in red-backed vole's diet (Dykes , 1971;Maser *et al*, 1978;Martell, 1981;Ovaska and Herman, 1986;Maser and Maser, 1988).

As for meadow voles (*Microtus pennsylvanicus*), they are typical inhabitants of prairie habitat types (Grant and Birney, 1979) such as grass and wet meadows (Getz, 1961;Clough, 1964;Reich, 1981;Hallet *et al*, 1983;Galindo and Krebs, 1985). Studies in the Yukon conducted in tundras, forests, shrublands and marshes found the highest

density of meadow voles in marsh-type habitats (Olsen, 1968;Krebs and Wingate, 1976). Numerous authors have noted that grass cover was an important feature in microhabitat of meadow voles (Hallet *et al*, 1983;Durst, 1984;Galindo, 1984;Linzey and Cranford, 1984;Thurber and Herman, 1984;Adler, 1985;Millar *et al*, 1985;Dueser and Porter, 1986;McGowan and Bookhout, 1986). Adler and Wilson (1989) have recently argued that a grass cover of 30-40% was essential for a viable meadow vole population.

Although meadow jumping mice (*Zapus hudsonius*) habitat preferences are similar to meadow vole (Whitaker, 1972;Hallet *et al*, 1983;Durst, 1984;Adler, 1985;Monthey and Soutiere, 1985), the dependence on herbaceous cover does not seem to be as vital. Using discriminant function analysis (a statistical analysis by which the main factors differentiating habitat characteristics of two species can be measured), Porter and Dueser (1982), showed that the habitat niche of meadow jumping mice was intermediate between those of deer mice and meadow voles in terms of shrub and herbaceous cover. Dueser and Porter (1986) observed the highest density of meadow jumping mice in shrubland with susbstantial herbaceous cover. Grass bordering streams and ponds could also offer favorable habitats (Whitaker, 1963).

Based on the existing literature, it can be hypothesized that the changes in vegetation from grass meadows to drier willow shrubland vegetation type should have a negative impact on meadow vole and meadow jumping mouse populations and a positive effect on deer mouse and red-backed vole populations. The general objective of this research was to evaluate the effect of the invasion of grass meadows by willow vegetation types on populations of small cricetinid and zapodid rodents in the Peace-Athabasca Delta.

The specific objectives were:

1) To verify if populations of small cricetinid and zapodid rodents present in adjacent young willow and grass meadow vegetation types of the Peace-

Athabasca Delta would show a pattern of habitat use similar to that described in the literature.

2) To obtain estimated population levels for species of small cricetinid and zapodid rodents in adjacent young willow and grass meadow vegetation types.

3) To evaluate the change in biomass due to the recently estimated vegetation changes that have and will take place in the Delta.

Methods

The study sites

The Peace-Athabasca Delta, situated within Wood Buffalo National Park (Figure 1), covers more than 4500 km2 (Doherty, 1978). The general topography is typical of a delta plain with a gentle relief broken by precambrian outcrops on the eastern edge. Nevertheless, the microtopography of a few meters is sufficent to dictate vegetation distribution in the Delta (Dirschl *et al*, 1974).

The completion of the W.A.C. Bennett Dam in 1968 and the subsequent construction of control dams in the Delta have drastically affected the hydrological regime, causing a decrease in the frequency of peak floods (Reinelt, 1971) and a drying up of a number of perched basins (Peace-Athabasca Delta Project Group, 1973). Before the completion of the dam, the periodic floodings of the basins, besides favouring the maintenance of high biological productivity (Reinelt, 1971), helped to prevent the invasion of herbaceous vegetation by woody species (Peace-Athabasca Delta Project Group, 1973).

Lands frequently flooded in the Delta are characterized by a mix of emergent aquatic plants, sedges and grasses with large areas colonized by awned sedge *(Carex atherodes)* or reed grass *(Calamagrostis spp.)*. Willow vegetation type (*Salix* spp) is common along streams and channel levees. On the older and upper parts of the Delta, forests of white spruce *(Picea glauca)* and balsam poplar (*Populus balsamifera)* are frequent (Raup, 1935).

Three study sites were selected along the Prairie River between Lake Claire and Lake Mamawi (Figure 2). The selection was based on satellite images, vegetation maps and previous vegetation studies (Dirschl *et al*, 1974;Jaques, 1990). The three

Figure 1. The Peace-Athabasca Delta Area

(SCALE 1/ 10 000 000)

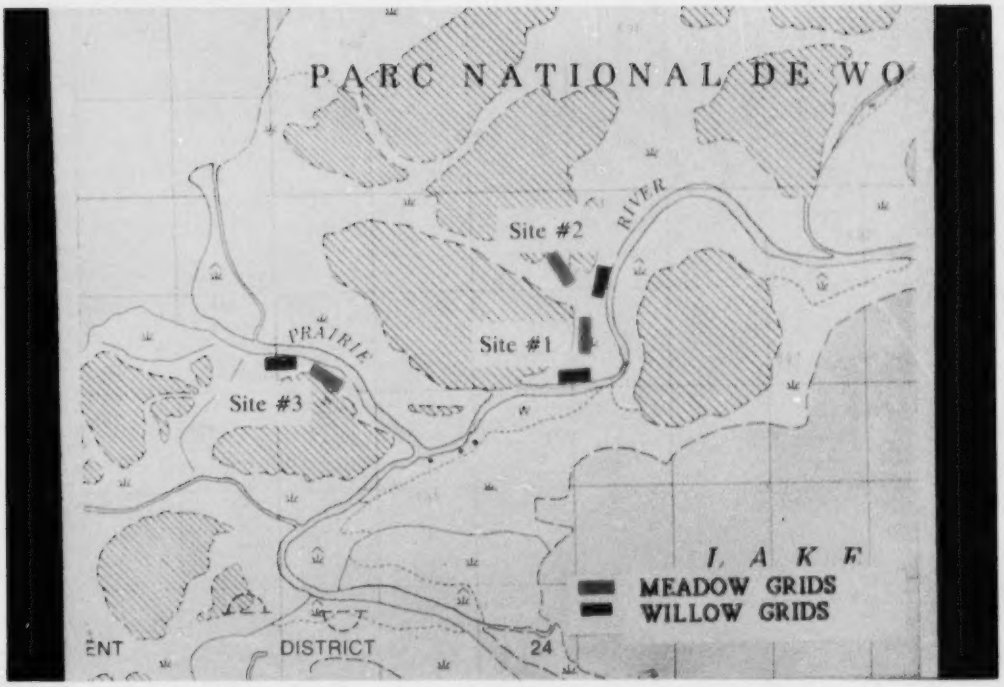


Figure 2. The study sites along Prairie River located at 58° 38' N. and 111° 39' W. (SCALE 1/ 60 000)

sites were located in areas where willow invasion has been extensive since 1968 (Figure 3 and 4), and where there were adjacent young willow and grass meadow vegetation types. Vegetation description was done by visual observations.

Salix bebbiana and *Salix interior* dominated the upper vegetative layer in the willow grids. Since distinct microhabitats existed within the willows grids, vegetation characteristics were described separately for each of those microhabitats. Diagrams representing the importance and locations of each microhabitat within the three willow grids and a detailed list of species are given in Appendix I and II. The microhabitat designated as old grove willow is characterized by 25 to 40 years-old willows about 5 meters high, and a substantial leaf litter (Figure 5). The microhabitat called dense willow (Figure 6) refers to 10 to 13 years-old willow formations about 3 to 4 meters high, growing either over a dense herbaceous understory or a sparse one under which dead leaf litter was found. The age of willows in the interspersed willow microhabitat (Figure 7) is about the same as those found in dense willow, but willows are only about 2 to 3 meters high and sparsely distributed within a shrubby understory of *Cornus stolonifera* and *Rosa acicularis* . In some cases, the shrubby cover is replaced by a dense layer of *Equisitum arvense* (site#1) or herbaceous plants (site#3). Willow cover is negligible in the clearing microhabitat that occupies about 6% of the area of the willow grids (Figure 8). The main species composing the grass and herbaceous cover in the willow grids are *Calamagrostis canadensis, Rubus idaeus, Epilobium angustifolium* and *Anemone canadensis* . *Equisitum arvense* can also occupy a substantial proportion of the understory in some cases. Combined *Salix, Cornus* and *Rubus* cover in the three meadow grids ranged from 90 to 95% in old grove willow, 70 to 90% in dense willow, 35-70% in interspersed willow and 20-40% in clearing

Grass meadow grids were still markedly different from the four microhabitats present in the willow grids though (Figure 9). Total cover in the meadow grids varied from 75% (site #2 and #3) to 80% (site #1). The dominant species were grasses as

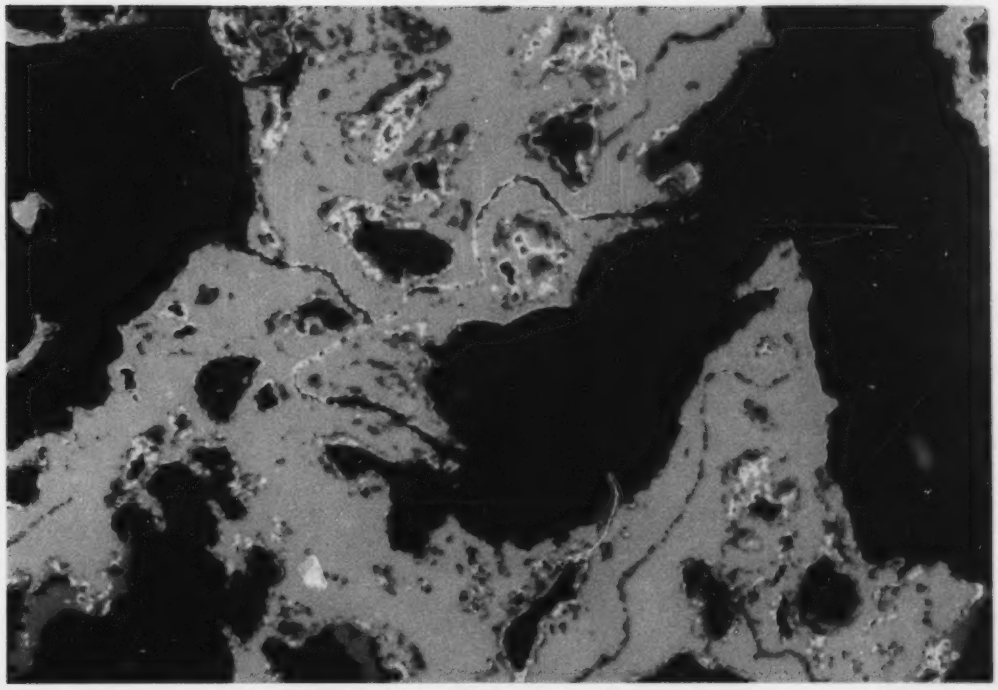


Figure 3. Main vegetation types in the Prairie River Area of the Peace-Athabasca Delta in 1970 (SCALE IS ABOUT 1/ 110 000)

Colour codes are:Red=Forest & tall shrub;Green=Low shrub;Yellow=meadows; Light blue=Immature fen;Orange=Emergents;Dark blue=Water

PHOTO ADAPTED FROM JAQUES (1990)

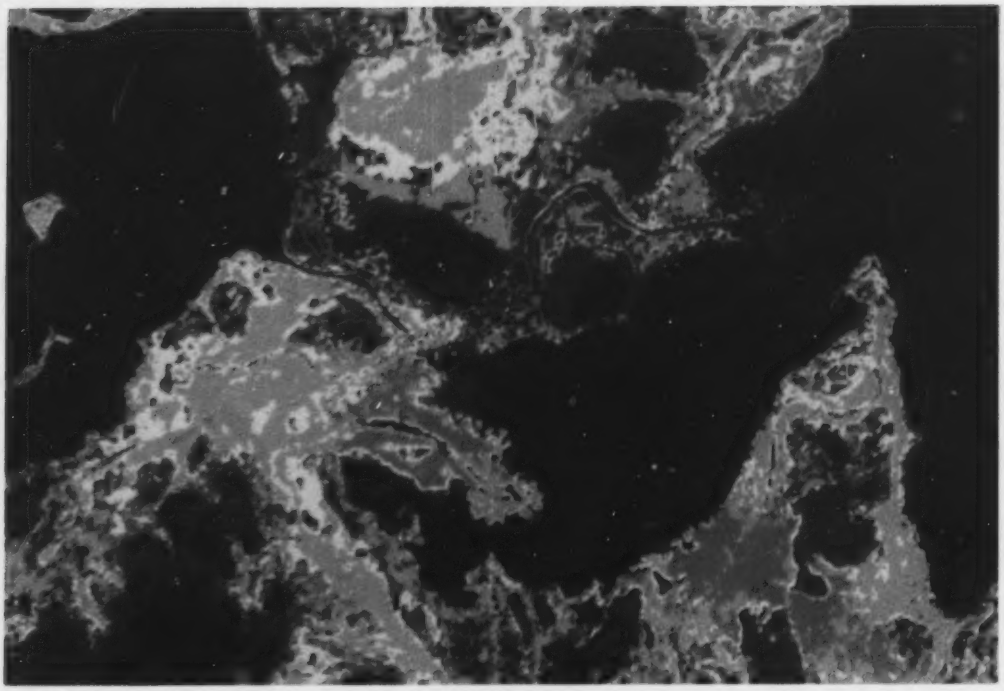


Figure 4. Main vegetation types in the Prairie River Area of the Peace-Athabasca Delta in 1989 (SCALE IS ABOUT 1/ 110 000)

Colour codes are:Dark green & navy blue=Forests;Red=Tall shrublands;Medium green=Low shrublands;Gray, purple & orange=Meadows;Turquoise=Emergents; Medium dark blue=Water

PHOTO ADAPTED FROM JAQUES (1990)

Figure 5. Old grove willow in the willow grid of study site #3 showing low density understory

Figure 6. Dense willow with an herbaceous sub-story in the willow grid of study site #2 showing a dense willow cover of about 80%

Figure 7. Interspersed willow in the willow grid of study site #3 with a heavy understory cover of *Rosa acicularis*

Figure 8. Clearing in the willow grid of study site #1 showing a moderate shrub cover

Figure 9. Meadow grid at study site #1 showing a grass cover dominated by *Calamagrostis canadensis*

opposed to sedge-dominated meadows. *Calamagrostis canadensis*, had a cover of 20 to 40% in site #1, 60 to 80% in site #2 and 40 to 60% in site #3. *Cina latifolia, Poa palustris, and Phalaris arundinacea* were the other grass species with a cover of at least one to five percent in one or more of the meadow grids. Other important plants also present included *Cirsium arvense, Anemone canadensis Sonchus arvensis, Rubus idaeus* and *Epilobium angustifolium*.. A detailed list of species is given in Appendix III.

Monitoring of small mammal populations

Two grid patterns, each 165m x 45m, were located at least 300 m apart in adjacent willow and grass meadow vegetation types in each of the three study sites. In each grid, 24 live traps were located 21.2 meters apart from each other in a sytematic way along the grid lines as indicated in Fig. 10. All traps were prebaited for 5 days before the first trapping session so small mammals would become habituated to the traps. Each site was trapped for a period of about 17 hours every 6 or 7 days. Traps were set at about 3 P.M. checked at about 8 or 9 P.M. and re-checked at about 6 or 7 A.M. the following morning. This method provided adequate trapping time for diurnal and nocturnal animals and helped to avoid death by exposure. Ear puncher and dye (between the anterior and posterior pairs of legs) were used to mark captured animals.

The Jolly-Seber mark-and-recapture method (Krebs, 1989) and the minimum number known alive (M.N.A.) method (Hilborn *et al*, 1976) were used to estimate populations by species in willow and grass meadow grids. Because of difficulties in trapping juveniles and subadults due to their small weight, adult and juvenile/subadult population densities (obtained from M.N.A. population estimates on

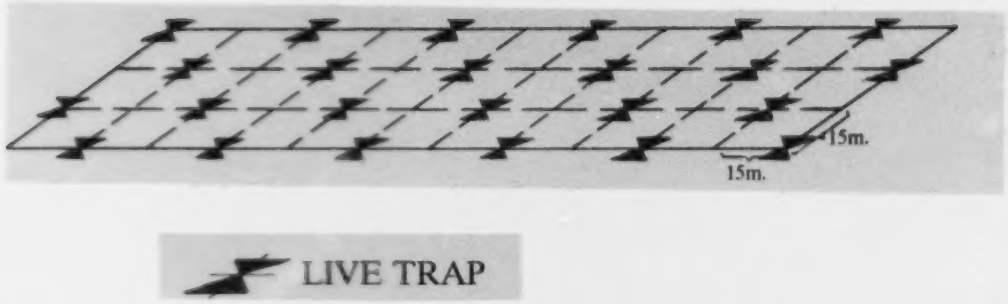


Figure 10. Location of the live traps on the trapping grids

the trapping grids) were computed separately (for reference to weight classification see Sullivan, 1976;Gilbert and Krebs, 1981;Boonstra and Krebs, 1979; Whitaker, 1963), and only the adult populations were used when conducting statistical tests or evaluating biomass changes. The fact that both methods are designed for open populations allowed their sampling during a period of eight trapping sessions (about a month-and-a-half). The trapping schedule also ensured that the sampling time was negligible as compared to the intervals between samplings -an assumption of the Jolly-Seber method- (Krebs, 1989).

To calculate biomass for each small mammal species in both willow and grass meadow grids, the mean weight of adult males and females captured over the three study sites was multiplied by the mean of the population estimates obtained by the M.N.A. method in willow and grass meadow grids over the three study sites. M.N.A. population estimates were used rather than Jolly Seber since the latter estimates were unavailable for meadow jumping mice and meadow voles caught in the willow grids.

Statistical analysis

As population estimates were not normally distributed (the absence of deer mice and red-backed voles in at least two of the three meadow grids and the absence of adult meadow voles in all but one of the willow grids strongly skewed the distribution), a Mann-Whitney test was performed to compare population estimates between willow and meadow grids obtained over the three study sites for each species. Mean M.N.A. population estimates obtained in willow grids were compared to those obtained in meadow grids to verify if trends in populations of deer mice, red-backed voles and meadow voles were statistically significant.

One factor that might have influenced density estimates is the so-called "edge effect". To test if edge effect was actually occuring in the grids, individual trap sites were either classified as "outer traps" (all the traps situated on the border of the grid) or "inner traps". The percentage of outer traps (58.33% or 14 out of 24 traps) and inner traps (41.67% or 10 out of 24 traps) was then multiplied by the total number of captures for each species on each grid to generate an expected frequency of captures at outer and inner trap sites. This expected frequency was compared to the observed frequency in the field in a series of G tests. Meadow voles in willow grids were not included since they were considered as a transient population. Meadow jumping mice were discarded because of their limitation to one microhabitat type at study site #3.

A similar procedure was used to measure differences in microhabitat uses between red-backed voles and deer mice. It was hypothesized that old grove willow would be the microhabitat most heavily used by red-backed voles whereas dense willow and interspersed willow would be the microhabitat most often use by deer mice. A G test was done to compare the occurence of observed and expected captures of the two species within each microhabitat of the willow grid at site #3. Site #1 and #2 were discarded because of the high number of traps straddling two microhabitats at site #1 and the absence of the red-backed vole's hypothesized preferred microhabitat (old grove willow) at site #2. First, to verify that hypothesis, the percentage of traps located within each microhabitat was calculated (Appendix I). These percentages were then multiplied by the total number of captures of deer mice and red backed voles in the willow grid at site #3 to generate an expected frequency of captures within each microhabitat for each species. This expected frequency was compared to the observed frequency in the field. To compensate for small sample size, William's correction was used (Sokal and Rohlf, 1981).

Results

Populations

The data illustrate the very clear trend that was observed in the field. Adult deer mice, red-backed voles and meadow jumping mice used the willow grids exclusively whereas adult meadow voles were restricted mainly to the grass meadow grids (Table 1). Thus, the patterns observed in this study are generally in accordance with results described in the literature.

Population estimates calculated by the M.N.A. and Jolly-Seber method for the adult segment of the population are presented in Table 2. As in Table 1, the trend noticeable between willow and meadow grids is very clear. Population estimates were fairly similar for the same species over the three study sites and differences tended to be more noticeable between willow and meadow grids than between study sites. Computations for the total population and the juvenile/subadult segment of the population for the Jolly-Seber method are given in Appendices IV and V.

Since all sites showed the same trends over the meadow and willow grids, the Mann-Whitney tests for each species were both identical and statistically significant ($P<0.05$).

$U_{STATISTICAL} = 15$

$U_{3,3\ CRITICAL} = 9$

The results for the G tests to verify edge effect were all strongly not significant ($p<0.9$) except in the case of the meadow voles in the meadow grid of study site #1 ($p<0.05$). Thus edge effect did not play an important role in most cases. In view of the conclusive G test, however, only data from site #2 and #3 were used to calculate biomass of meadow voles in grass meadow grids.

Table 1. Number of adult individuals caught in the willow and meadow trapping grids (28 May to the 15 July 1991) by species at the three study sites (not counting recaptures)

	SITE #					
	1		2		3	
SPECIES	Willow	Meadow	Willow	Meadow	Willow	Meadow
Deer mice	8	-	12	-	19	-
Red-backed voles	8*	-	8	-	8	-
Meadow jumping mice	-	-	-	-	5	-
Meadow voles	1	57	4	41	2	44*

* = # of mortalities during manipulation or subsequent to it (the mortalities are included in the totals)

Table 2. Mean trapping estimates (± standard error) and trappability from minimum number known alive method and mean trapping estimates (± standard error) and mean survival rates from the Jolly-Seber method on the trapping grids from small mammals captured between the 28th of May and the 15th of July 1991

	Site # 1		Site # 2		Site # 3	
SPECIES	Willow	Meadow	Willow	Meadow	Willow	Meadow
Deer mice						
Trap. est.(M.N.A.)	2.5(±.5)	0	4.0(±.9)	0	6.8(±1.7)	0
Trappability (%)	67		96		80	
Trap. est.(Jolly)	2.0(±0)	N.A.	4.5(±1.4)	N.A.	8.5(±1.9)	N.A.
Survival rates (%)	100		81		78	
Red-backed voles						
Trap. est.(M.N.A.)	2.7(±.8)	0	4.8(±2.4)	0	5.0(±.6)	0
Trappability (%)	92		91		85	
Trap. est.(Jolly)	2.9(±.7)	N.A.	5.7(±1.6)	N.A.	5.1(±0.8)	N.A.
Survival rates (%)	81		86		88	
Meadow jumping mice						
Population est.	0	0	0	0	0.7(±.5)	0
Trappability (%)					67	
Meadow voles						
Trap. est.(M.N.A.)	.2(±.4)	23.5(±4.3)	.8(±1)	20.8(±4.7)	.3(±.5)	18.3(±2.5)
Trappability (%)	17	74	50	71	33	73
Trap. est.(Jolly)	N.A.	32.2(±5.3)	N.A.	29.8(±7.3)	N.A.	23.2(±3.1)
Survival rates (%)		84		91		81

N.A. = Non available data due to insufficient number of recaptures

Biomass

Mean weight and mean population estimates and biomass are given in Table 3 and 4, respectively. The biomass in meadow grids was about four times that of willow grids. The greater biomass was due not only to higher densities of small cricetinid and zapodid rodents but also to the fact that meadow voles captured in willow grids were noticeably heavier than red-backed voles and deer mice.

Microhabitat uses

Microhabitat uses could certainly affect the evolution of the distribution and the relative importance of small mammal populations in the Delta. Therefore the examination of microhabitat uses is necessary to predict future trends in small mammal populations in the Delta with more confidence and precision.

Observed and expected rates of captures in microhabitats that were hypothesized to be the most heavily used by deer mice did not yield statistically significant results (Appendix VI). As for red-backed voles, there was a tendency (although not statistically significant) for a more important use of old grove willow as compared to dense and interspersed willow. Out of eight captures of red-backed voles in the willow grid of study site #3, four occured in old grove willow while we would have expected to capture only two individuals in that microhabitat (Appendix VI).

Table 3. Weight in grams (X±S.E.) of adult males and females (pregnant and non-pregnant) by species over the three study sites in willow and meadow grids

SPECIES	HABITATS	Weights	n (sample size)
Deer mouse	Willow	22.1 ±2.9	38
Red-backed vole	Willow	22.9 ±2.5	22
Meadow jumping mouse	Willow	17.8 ±2.4	5
Meadow vole	Willow	33.8 ±2.9	5
	Meadow	37.4 ±4.8	123

Table 4. Mean population estimates and small mammal biomass (X± S.E.) in willow and meadow grids (g./0.74 ha.) by species

	Willow	Meadow
Deer mice		
Population	4.4 ±2.1	-
Biomass	97.2 (50.8 - 143.65)	-
Red-backed voles		
Population	4.2 ±1.8	-
Biomass	96.2 (55.0 - 137.4)	-
Meadow jumping mice		
Population	0.2 ±0.4	-
Biomass	3.56 (0 -10.7)	-
Meadow voles		
Population	0.4 ±0.7	20.9 ±4.3
Biomass	13.5 (0 - 37.2)	781.7 (620.8 - 942.5)
Total biomass	**210.5 (105.8 - 328.95)**	**781.7 (620.8 - 942.5)**

Discussion

Microhabitat and habitat uses

Even though it appears that red-backed vole and deer mouse populations will be favoured by the vegetation changes taking place in the Delta, the question of the relative importance of the increase between the two species should be examined more closely.

Although a more important use than expected of old grove by red-backed voles was noticed in the G test regarding habitat use, no conclusive results (statistically speaking) could be obtained. The question of testing if this heavier use is an indication of microhabitat preference also remains unanswered. A bigger sample size might have given more conclusive results. In any case, if the preference of red-backed voles for more mature types of formations as reported elsewhere (Miller and Getz, 1972) also holds true in the Peace-Athabasca Delta (an hypothesis that remains to be proven), then the vegetation successional trends that have been observed so far in the trapping grids could favour red-backed voles over deer mice. The absence of an abundant herbaceous or shrub cover (in particular of *C. canadensis*) and vertical cover in old grove willow microhabitat should, in theory, negatively affect deer mice. On the other hand, greater arboreal cover, moister conditions and the presence of an abundant leaf litter in that microhabitat should, still in theory, favor red-backed voles. Red-backed voles often forage and burrow under leaf litter (Gunther *et al*, 1983;Ovaska and Herman, 1986). The dense willow cover of old grove willow could easily compensate for the lack of ground cover and offer more favorable growth conditions to the red-backed vole's main food item. Stock (1976) captured a substantial number of red-backed voles in habitats with dense overstory even if the ground cover was sparse.

In the case of meadow voles , a massive colonization of willow habitat by this species in the coming years (if we except peak meadow vole years) seems at best improbable considering that the herbaceous cover was often below 40% in willow grids (in particular for old grove willow type of microhabitat).

As for the absence of captures of meadow jumping mice in meadow grids and its presence in only one willow grid, part of the explanation could be related to the occurrence of a specific microhabitat in site #3 that will probably become increasingly rare as the colonization process continues. All of the captures at site #3 were in interspersed willow with an important herbaceous cover. Furthermore, these interspersed willows were joined by a narrow corridor to a grass meadow (a type of transition area). Qimby (1951) noted the presence of meadow jumping mice in transition areas between willow-alder thickets and grass marshes.

The effect of high density years of meadow voles and red-backed voles on habitat uses will probably alter the patterns observed in this study with meadow voles and red-backed voles temporarily invading willow and meadow grids respectively. However, in years of low density of meadow voles and red-backed voles , the general pattern observed in this study should hold.

Densities and annual fluctuations

Since data were collected for only one summer, the densities obtained from population estimates should be examined with caution.

One of the main assumptions of the Jolly-Seber method concerns equal catchability. However, the bias produced by that assumption becomes relatively unimportant if the trappability of the population exceeds 50% (Hilborn *et al*, 1976). The

trappability figures in table 2 were usually around 70-80%, with the exception of deer mice at site# 1.

But even when population estimates are fairly accurate, the use of densities obtained from population estimates to assess habitat preferences can be misleading since high population densities and low survival can be found in marginal habitats (Van Horne, 1982). However, the fact that habitat uses by each species observed in this study were so clear and that turnover rates did not seem to be excessive (see survival rates in Table 2) indicates that this is unlikely to have been the case.

A notable exception to that general pattern though can be found if we look at the meadow voles that were captured in the willow grids. Although no survival rates could be calculated, some demographic characteristics of those meadow voles were markedly different from meadow voles captured in meadow grids. One striking pattern that emerged from meadow voles captured in willow grids is that most of them were either juveniles or subadults at the time of their first capture (75.5% of the total population in willow grids compared to 42% in meadow grids). In addition, only a small fraction of the meadow voles captured in the willow grids were subsequently recaptured (25.5% compared to 54% in meadow grids). One of the possible explanations for these patterns is that most of those individuals were transient juveniles or subadults from the nearby meadows. The number of those transient individuals should theoratically increase in years of high meadow voles densities (Morris, 1984;Boonstra and Craine, 1988;Brochu *et al*, 1988). A last piece of evidence that further strengthens this possible explanation is that almost all of the captures of meadow voles in willow (67%) occurred at the outer edge of the grid that was the closest to the meadows.

Thus it seems that not only will red-backed vole and deer mouse populations strongly increase due to changes in the vegetation (with, possibly, the relative importance of red-backed voles increasing over deer mice) but that these vegetation

changes will also result in a decrease in meadow voles to a significantly reduced population level.

The incidence of annual variations on the representativeness of population estimates calculated in this study should not have an important effect on deer mice because they are generally considered to be non-cyclic (Krebs and Wingate, 1985;Van Horne, 1982). The densities reported here might then accurately reflect the average density found in the field. In regards to red-backed voles, densities measured in the Northwest Territories ranged from 0 to 54 individuals/ha. (Fuller, 1969, 1977;Mihok, 1979) while they reached a maximum of 22 individuals/ha. in Alberta (Kucera and Fuller, 1978). As for meadow voles, it is doubtful if their densities will noticeably decrease but a four-fold increase in density per hectare is quite possible. Measured densities of meadow voles usually have not fallen below 20 individuals/ha. (Anthony *et al*, 1981[modified Schnabel estimator -Overton, 1965-];Boonstra and Rodd, 1984) while population estimates recorded near Saskatoon ranged from 65 voles/ha. to a maximum of 118 voles/ha. (Morris, 1969). Thus, both populations of red-backed voles and meadow voles seemed to be in a low population phase when this study was conducted (although red-backed voles were not in their optimum habitat according to the literature) and could experience substantial increase in numbers. The potential of biomass increase seems to be greater for meadow voles than red-backed voles though if we consider maximum densities reported elsewhere and the heavier weight of meadow voles. Thus, actual changes in biomass if they differed from those predicted in this study will probably be even more important. Biomass figures calculated in this study should still be valid though (at least in low density years of meadow voles and red-backed voles) and could be used as a benchmark in more long-term studies.

Another potential source of variation is the possibility of a discrepancy between densities of small cricetinid and zapodid rodents measured in the Prairie River Area of the Delta and those occuring in other parts of the Delta. Thus, the estimated change

of biomass presented in this study should in no way be interpreted in terms of absolute numbers.

Vegetation shift and small mammal biomass

Willow grids had a higher diversity than meadow grids since two or three (site #3) species of small cricetinid and zapodid rodents were captured in meadow grids while only meadow voles were captured in meadow grids. Thus, in the coming years, the diversity level will probably increase in the meadow areas being colonized by young willows.

The scope of the vegetation changes in time and space taking place in the Peace-Athabasca Delta was demonstrated by a recent remote sensing study (Jaques, 1990). From 1970 to 1989 the expanse of meadows in the Delta (including grass and sedge meadows) decreased from 16.5% to 12.6% while tall shrubs and forests increased from 20.4% to 26% of the total delta area. According to the same report, within 2 to 4 decades, the productive meadow habitat types could be largely replaced by shrub-dominated habitats.

By combining these vegetation type changes with the small mammal biomass estimates, we can suggest that the disappearance of meadows and its replacement by young willow formations within the next two to four decades will result in a biomass loss of small cricetinid and zapodid rodents of about 56% of the biomass that was formerly present in the area colonized (Table 5)

The main assumption of these calculations is that the population level of species found in sedge meadows will be similar to those observed in grass meadows. More precisely, this would mean that meadow voles would constitute the almost sole representative of small cricetinid and zapodid rodent species in sedge meadows.

Table 5 Estimated long-term changes in biomass of small cricetinid and zapodid rodents in the Peace-Athabasca Delta based on estimated vegetation changes by Jaques (1990) and population estimates from the present study

Year	Net Biomass Loss (kg)	Loss of Biomass Compared to Biomass Present in Meadows in 1976
1976 - 1989	X = 14 196 kg	17%
	Min = 12 800 kg	16%
	Max = 15 250 kg	18%
1989 - 2011	X = 48 864 kg	56%
to 2028	Min = 41 353 kg	50%
	Max = 49 270 kg	60%

Net Biomass Loss = Estimated number of ha. of grass and sedge meadows colonized by willows x net difference of biomass per ha. between meadow and willow sites

Biomass Present in Meadows in 1976 = Mean biomass per ha. found in the meadow site x estimated number of ha of grass and sedge meadows present in the P.A. Delta in 1976

Loss of Biomass Compared to Biomass Present in Meadows in 1976

$$= \frac{\text{Net Biomass Loss}}{\text{Biomass Present in Meadows in 1976}}$$

Although no experimental evidences were collected to confirm this in the present study, this is likely to be the case since sedge meadows are similar, in structure, to grass meadows and have often been shown as one of the prime habitats of meadow voles (Findley, 1954;Krebs and Wingate, 1976;Galindo and Krebs, 1985). As for population levels of meadow voles, it is very unlikely that densities found in sedge meadows would be lower than those found in grass meadows since meadow voles' densities in grass meadows already appear to be low. Thus , once again, forecasted changes in biomass could well be more important.

Food web implications

The rapid turnover rates of small mammals' biomass (high reproduction, low survival) makes them important and often readily available prey for a number of predators (Hayward and Phillipson, 1979). Almost all mustelids including marten - *Martes americana* - (Lensink *et al*, 1955;Murie, 1961;Weckwerth and Hawley, 1962;Douglass *et al*, 1983;Gordon, 1986), ermine - *Mustela erminea* - (Raymond and Bergeron, 1986) and least weasel - *Mustela nivalis* - (Banfield, 1974) and a good proportion of birds of prey including red-tailed hawk (*Buteo jamacensis*), short-eared owl (*Asio flammeus*) and american kestrel (*Falco tinnunculus*), as reported by Baker and Brooks (1981), Salt and Salt (1976) and Anderson and Erlingue (1977) depend heavily on small mammals. Fox (*Vulpes* spp.) and coyote (*Canis latrans*) also prey on small mammals (MacCraken and Hansen, 1986;Kaikusalo, 1982 ; Hoffman, 1979).

It appears from the literature that vole species are a preferred prey for mammalian predators - in particular ermine (Simms, 1979;Raymond and Bergeron,

1986) - while deer mice is often disdained by them (Soutiere, 1979). In fact, deer mice seem to have a low palatability to ermine (Nams, 1981).

This decrease of small mammal biomass predicted for the Delta will probably strongly affect the productivity of raptors. Much evidence suggests that small mammal abundance and productivity of raptors (Korpimäki, 1985;Simmons *et al.* ,1986) fox (Kaikusalo, 1982) as well as mustelids (Hamilton, 1933;Parovschchikov, 1963;Tapper, 1979;Raymond and Bergeron, 1982) are closely linked.

Very few studies on predator densities have been completed in the Delta. An indirect method of studying the effect of the changes in small cricetinid and zapodid rodents biomass on predators is to examine trapping records for the Wood Buffalo National Park Area. Figure 11 presents the number of weasel and ermine pelts sold - two of the most typical vole specialists in the mustelid family (Anderson and Erlinge, 1977;Simms, 1979;Raymond and Bergeron, 1986) -, while Figure 12 presents the ratio of the number of weasel and ermine pelts sold divided by the number of trappers having a fur sale record. The appellation weasel in these figures include weasel and ermine. The number of trappers selling pelts was used to estimate trapping effort. In both figures, the data were computed for trapping areas within and adjacent to the Peace-Athabasca Delta (Appendix VI).

Populations within and adjacent to the Peace-Athabasca Delta area fluctuated approximately in synchrony and there was a strong decrease in number since the 1966-67 trapping season (although it might have occured earlier since data from 1959 to 1966 are missing). A similar pattern was observed in the trapping returns of weasel pelts in the rest of Alberta with a sudden decrease around the 1960's. What is particularly intriguing is that the decrease occurred before the completion of the Bennett Dam. Part of the explanation may relate to the decrease of trapping efforts since the price of weasel pelts, in spite of recent increases, has not kept pace with inflation. The general decrease of trapping effort in the Delta (in particular for muskrats) might have also played a role

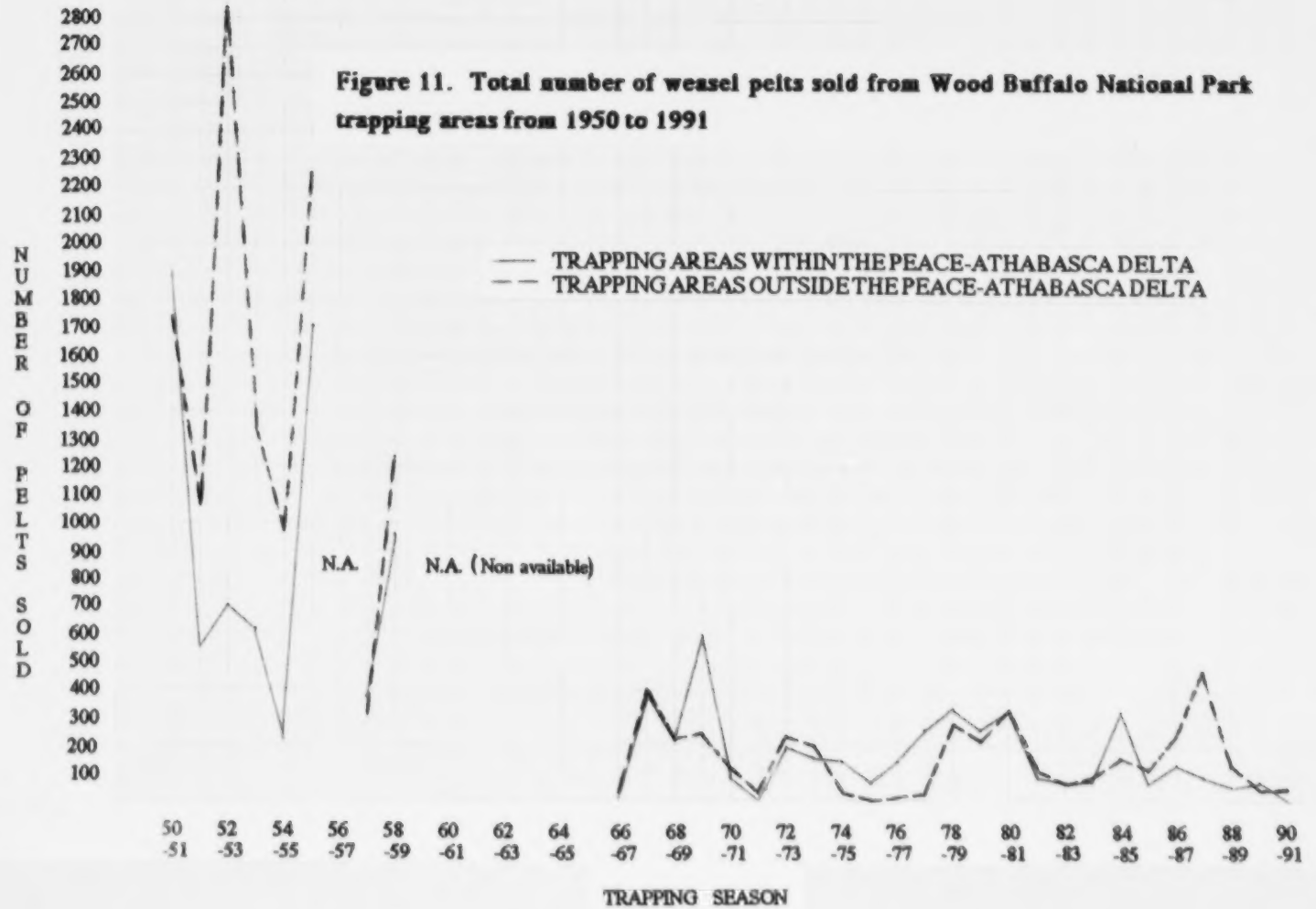
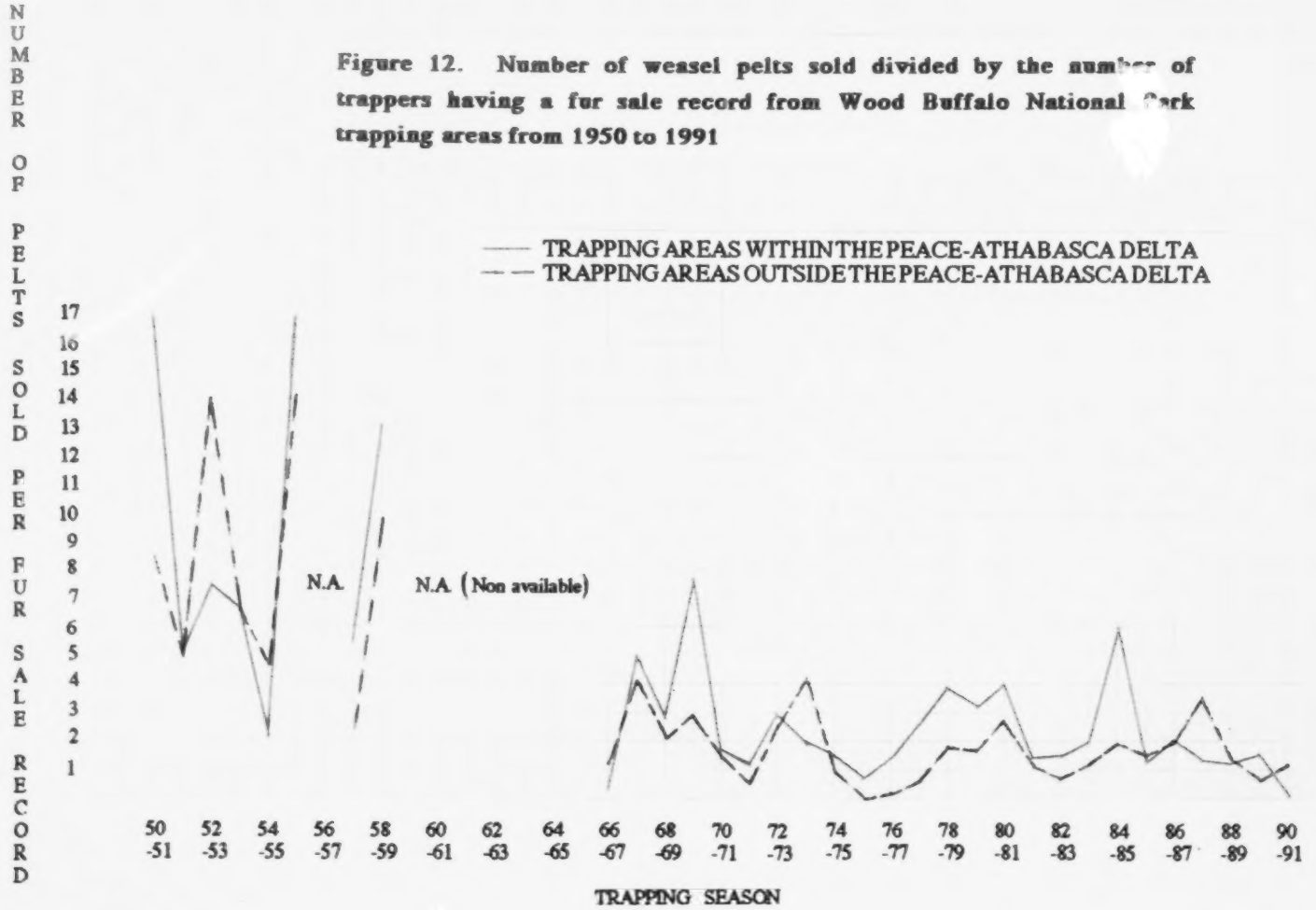


Figure 11. Total number of weasel pelts sold from Wood Buffalo National Park trapping areas from 1950 to 1991

Figure 12. Number of weasel pelts sold divided by the number of trappers having a fur sale record from Wood Buffalo National Park trapping areas from 1950 to 1991



since weasels were often trapped as a complement to other more economically important species. However, the drop in the ratio of weasel pelts to trappers indicates that the weasel population may well have declined in recent years. Although no definitive fluctuation patterns in trapping returns of weasel could be linked to the decrease in biomass of small cricetinid and zapodid rodents calculated in this study since 1966-67, the more substantial changes that are forecasted in the coming years might possibly have an effect.

In terms of absolute number, this decrease of meadow vole populations will probably not be compensated by the increase in deer mouse and red-backed vole populations and could well be close to the minimum density of small mammals necessary for the subsistance of breeding female ermine (Erlinge, 1974).

Foraging efficiency of predators will also probably be affected. According to the optimal foraging theory, predators are supposed to partition their foraging time to optimize energy intakes (Mac Arthur and Pianka, 1966;Krebs, 1973;Smith and Sweatman, 1974;Zach and Falls, 1976;Pyke *et al.*, 1977;Bobisud and Voxman, 1979). Some researchers have in fact argued that predators learn to recognize the most advantageous patches in term of biomass of prey taken by unit of hunting time rather than those containing the greatest net biomass (Royama, 1970). Results obtained by numerous researchers have indicated that the main factor influencing raptor foraging would be cover density rather than prey density with a proportionally higher number of strikes occurring in habitats with low cover (Craighead and Craighead, 1956;Wakelly, 1978;Baker and Brooks, 1981;Bechard, 1982;Boxall and Lein, 1982).

Therefore, the impact on raptors of small mammal population changes in the Delta will probably be worsened by the parallel change in vegetation cover. This will affect raptors differently depending on their hunting technique. Raptors that usually hunt over prairie type habitat like northern harriers (*Cirus cyaneus*) and merlin (*Falco columbarius*) (Brown and Amadon, 1968) or short-eared owl (Burton, 1973) are likely

to be the most affected (although most owls that hunt over prairie type habitat still need to perch on some kind of edges or tree). The effect of the decrease in meadow voles biomass will be even more important if we consider the generalized preference of predators for meadow voles. Those two factors, along with an increase in fire severity and frequency in the Delta due to climate change (Hogenbirk and Wein, 1991), will worsen the impact that the diminution of small mammal biomass will have on predators.

Conclusion

The results of this study suggest that vegetation changes actually occurring in the Peace-Athabasca Delta have and will continue to have negative repercussions on small mammal biomass. Although these changes have and will continue to take place gradually over the next decades, they will nonetheless be quite substantial in terms of small mammal species diversity and biomass. Those changes should also have important implications for the food web of the Delta.

The disappearance of meadows in the Delta in two to four decades could lead to significant losses in the number of meadow voles from the Delta and a loss of more than 50% of the biomass of small cricetinid and zapodid rodents present in the newly colonized meadow. Predators (especially mustelids and raptors usually foraging over prairie type of habitat) should experience decreases in foraging efficiency and productivity. This negative impact could be lessened by the increase in relative importance of red-backed voles in the willow shrublands since there does not seem to be evidence (as it is the case between deer mice and meadow voles) of a preference for red-backed voles over meadow voles by mustelids.

The process of vegetation change appears irreversible unless a widely fluctuating water level regime is reestablished through the use of dams or ice jamming approaches. Wood Buffalo National Park is presently conducting some studies to evaluate these solutions. The question of the actual effect of small mammal fluctuations on their predators through population samplings and experimental manipulations of small mammals in the field could be worth investigating.

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APPENDIX I

Distribution of microhabitat types found in the willow grids

KEY

Old grove willow (*S. interior*)

Old grove willow (*S. bebbiana*)

Dense willow (*E. arvense*)

Dense willow (with dense herbaceous cover)

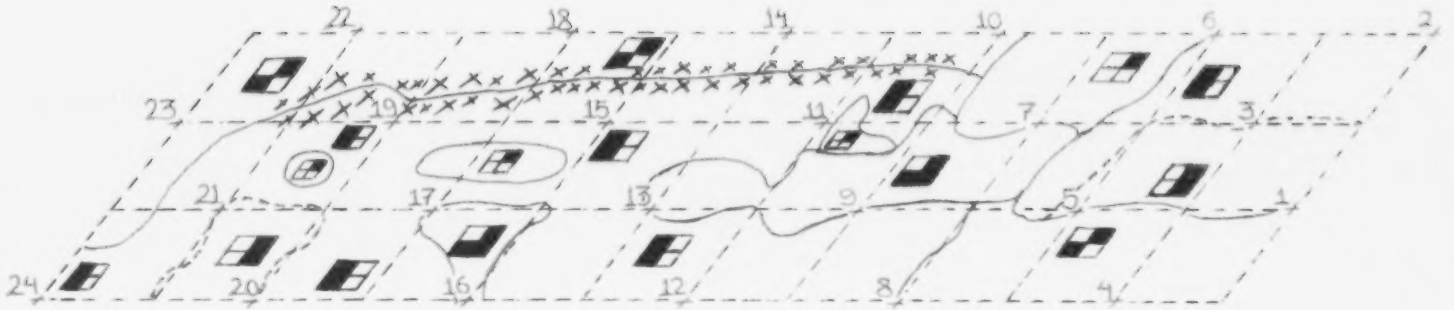
Interspersed willow (*C.canadensis*)

Interspersed willow (with dense herbaceous cover)

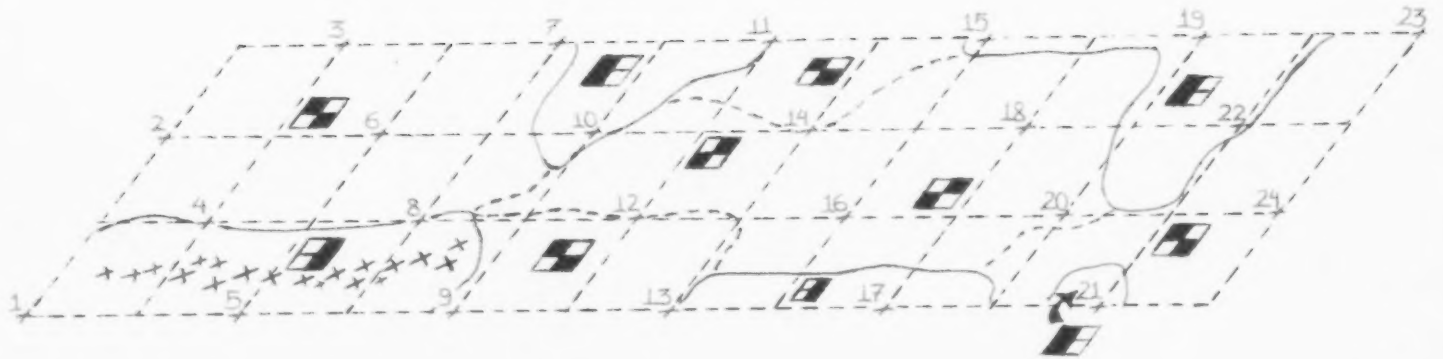
Clearing

Dead willows

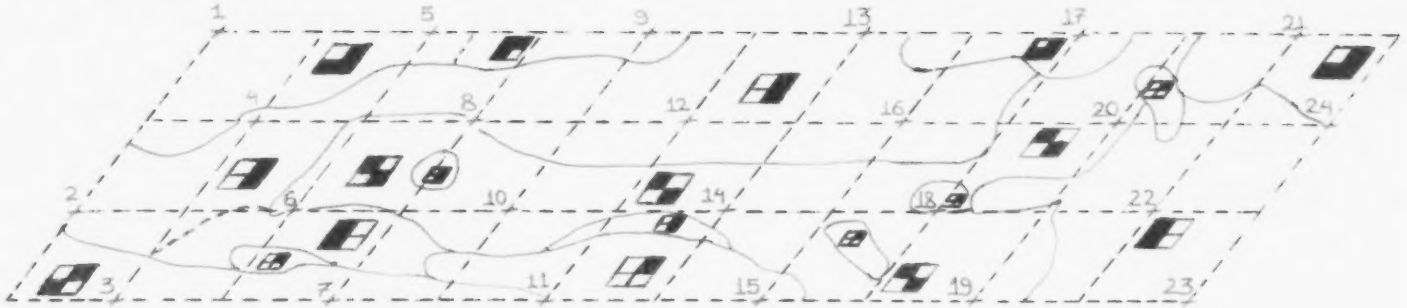
NUMBERS REPRESENT TRAP SITES



Meadow grid at study site # 1



Meadow grid at study site # 2



Meadow grid at study site # 3

APPENDIX II

Percentage cover of the plant species found in the willow grids

PLANT SPECIES **STUDY SITES**

OLD GROVE

	Site #1	Site #2	Site #3
Total overstory	80-100%	80-100%	80-100%
Salix bebbiana	80-100%	80-100%	60-80%%
Salix interior	0	0	5-20%
Total understory	20-40%	+	20-40%
Equisitum arvense	20-40%	+	20-40%
Cornus stolonifera (< 1.5 m.)	1-5%	0	1-5%
Rubus idaeus	0	0	1-5%
Chiogenes hispidula	0	0	+
Ribes triste	0	0	+
Dicranum spp.	0	0	+
Stellaria longifolia	0	0	+

DENSE WILLOW

	Site #1	Site #2	Site #3
Total overstory	80-100%	60-80%	60-80%
Salix interior	80-100%	60-80%	60-80%
Salix bebbiana	+	+	1-5%
Cornus stolonifera (> 1.5 m.)	0	+	0
Total understory	40-60%	20-40%	40-60%
Equisitum arvense	20-40%	5-20%	20-40%
Rubus idaeus	5-20%	5-20%	5-20%
Anemone canadensis	+	1-5%	5-20%
Calamagrostis canadensis	1-5%	+	1-5%
Vicia americana	+	1-5%	+

Cornus stolonifera (< 1.5 m.)	0	+	0
Stellaria longifolia	0	0	+
Sonchus arvensis	0	0	+
Cirsium arvense	0	+	0
Ribes triste	0	0	+
Potentilla anserina	0	0	+
Achillea sibirica	0	0	+
Epilobium angustifolium	+	0	0
Erigeron lonchophyllus	0	+	0

INTERSPERSED WILLOW

	Site #1	Site #2	Site #3
Total overstory	5-20%	20-40%	20-40%
Cornus stolonifera (> 1.5 m.)	5-20%	20-40%	20-40%
Salix interior	1-5%	1-5%	5-20%
Total understory	60-80%	60-80%	60-80%
Equisitum arvense	40-60%	1-5%	5-20%
Rosa acicularis	+	+	20-40%
Rubus idaeus	5-20%	5-20%	5-20%
Calamagrostis canadensis	5-20%	20-40%	1-5%
Epilobium angustifolium	+	1-5%	5-20%
Anemone canadensis	+	5-20%	+
Carex spp.	0	5-20%	0
Cirsium arvense	+	1-5%	+
Vicia americana	1-5%	+	+
Sonchus arvensis	0	1-5%	0
Ribes triste	0	0	1-5%
Ranunculus macounii	+	+	0
Stachys palustris	+	+	0
Stellaria longifolia	0	0	+
Potentilla anserina	0	+	0

Erysimum cheiranthoides	0	+	0
Ribes lacustre	0	0	+

CLEARING

	Site #1	Site #3
Total overstory	0	0
Total understory	80-100%	80-100%
Rubus idaeus	20-40%	20-40%
Calamagrostis canadensis	20-40%	20-40%
Equisitum arvense	+	20-40%
Epilobium angustifolium	5-20%	+
Anemone canadensis	5-20%	+
Sonchus arvensis	1-5%	1-5%
Cirsium arvense	1-5%	+
Ranunculus macounii	+	+
Urtica dioïca	+	+
Vicia americana	+	+
Stellaria longifolia	+	0
Potentilla anserina	+	0
Acillea sibirica	+	0
Cicuta maculata (var. *angustifolia*)	+	0
Erysimum cheiranthoides	+	0
Stachys palustris	0	+

APPENDIX III

Percentage cover of the plant species found in the meadow grids

PLANT SPECIES STUDY SITES

	Site #1	Site #2	Site #3
Total overstory	0	0	0
Total understory	80-100%	60-80%	60-80%
Calamagrostis canadensis	20-40%	60-80%	40-60%
Cina latifolia	20-40%	1-5%	5-20%
Poa palustris	5-20%	1-5%	+
Phalaris arundinacea	+	1-5%	0
Agrostis scabra	0	+	0
Cirsium arvense	5-20%	1-5%	+
Rubus idaeus	+	+	5-20%
Epilobium angustifolium	+	1-5%	1-5%
Anemone canadensis	1-5%	+	+
Sonchus arvensis	1-5%	+	+
Cicuta maculata (var. *angustifolia*)	+	+	+
Erisymum cheiranthoides	+	+	+
Stachys palustris (var. *pillosa*)	+	+	+
Ranunculus macounii	+	+	+
Stellaria longifolia	0	+	+
Urtica dioïca	+	+	0
Senecio pauperculus	+	0	+
Polygonum amphibium	0	+	+
Achillea sibirica	0	0	+
Potentilla anserina	+	0	0
Polygonum lapathifolium	0	+	0
Erigeron lonchophyllus	0	+	0

Mentha arvensis	0	0	+
Ranunculus sceleratus	0	0	+
Scutellaria gelericulata	0	0	+
Ribes lacustre	0	0	+
Sage spp.	0	0	+
Salix bebbiana (< 1m.)	+	0	+
Salix interior (< 1m.)	+	0	0

APPENDIX IV

Numbers of juveniles and subadults caught in the willow and meadow trapping grids (28th of May to the 15th of July 1991) by species at the three study sites (not counting recaptures)

SPECIES	SITE #					
	1		2		3	
	Willow	Meadow	Willow	Meadow	Willow	Meadow
Deer mice						
Juveniles	12	-	7	-	29**	1
Subadults	3	-	-	-	-	-
Red-backed voles						
Juveniles	3	-	3	-	1	-
Subadults	-	-	3	-	2	-
Meadow jumping mice						
Juveniles	-	-	-	-	-	-
Subadults	-	-	-	-	-	-
Meadow voles						
Juveniles	5***	26*	3	12	7*	8
Subadults	2	23	2	12	3	26

* = # of mortalities during manipulation or subsequent to it (the mortalities are included in the totals)

APPENDIX V

Jolly-Seber estimates of the total populations (adult, subadult and juvenile) of small mammals present at the three study sites

Site #1, Deer Mouse population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			0.625			0.319
2	0.429	8.8	0.688	2.9	4.1	0.384
3	0.6	8.9	0.545	-0.8	5.1	0.26
4	1	4	1	0	1.7	0
5	1	4	1.375	7.3	1.7	0.466
6	0.429	12.8	0.611	2.6	7.3	0.269
7	0.556	10.4			3.9	
8	0.667					

Site #1, Red-backed Vole population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			0.75			0.217
2	1	3	1	0.8	0.8	0
3	0.8	3.7	0.5	0.8	0.8	0.25
4	0.75	2.7	1	0.3	1	0
5	1	2	N.A.	N.A.	1.2	N.A.
6	0.667	6	N.A.	N.A.	N.A.	N.A.
7	0.4	2.5			N.A.	
8	0.8					

Site #1, Meadow Vole population (meadow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			0.25			0.217
2	0.222	4.5	1.13	49.2	0.9	0.083
3	0.167	54.3	1.04	24.1	18.3	0.149
4	0.432	79.5	0.612	17.2	15.9	0.095
5	0.514	65.9	1.174	11	9.9	0.168
6	0.676	88.4	0.661	4	15.8	0.128
7	0.75	62.4			10	
8	0.703					

Site #2, Deer Mouse population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			0.875			0.117
2	1	7	0.429	1.5	0.9	0.187
3	0.667	4.5	0.6	1	1.4	0.219
4	0.8	3.8	1	3.4	1.3	0
5	0.556	7.2	0.75	3.6	1.3	0.153
6	0.667	9	1	0.8	2.5	0
7	0.818	9.8			1.8	
8	1					

Site #2, Red-backed Vole population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			1			0
2	0.75	6.7	1	1.5	0	0
3	0.857	8.2	1.1	-0.2	0.7	0.135
4	1	8.8	0.682	0	1.1	0.192
5	1	6	1	2.6	1.2	0
6	0.7	8.6	0.667	2	1.2	0.157
7	0.778	7.7			2.5	
8	0.875					

Site #2, Meadow Vole population (meadow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			0.705			0.248
2	0.95	51.8	0.776	-13.2	40.5	0.104
3	0.688	27	0.979	14	5.3	0.08
4	0.56	39.4	0.939	3.9	6.4	0.081
5	0.759	41	1.103	12.3	5.3	0.188
6	0.731	57.5	0.594	-3.4	11.7	0.138
7	0.947	30.7			6.3	
8	0.692					

Site #3, Deer Mouse population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			0.952			0.191
2	0.625	10.7	0.793	2.5	2.7	0.209
3	0.7	11	0.609	4.2	2.4	0.192
4	0.6	10.8	0.692	5.2	2.7	0.204
5	0.545	12	0.812	9	3	0.296
6	0.5	18.8	0.665	14.2	8.7	0.226
7	0.333	26.8			6.5	
8	0.684					

Site #3, Red-backed Vole population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			0.8			0.179
2	0.833	4.8	1	1.2	0.9	0
3	0.833	6	1.033	0	1	0.068
4	1	6.2	0.806	1	1	0.177
5	0.833	6	1.048	3.1	1.3	0.074
6	0.667	9.4	0.754	-0.1	1.7	0.153
7	1	7			1.9	
8	1					

Site #3. Meadow Vole population (meadow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			N.A			N.A.
2	N.A	N.A	1.233	N.A.	N.A.	0.417
3	0.115	53.4	0.651	4.8	31.6	0.189
4	0.471	39	0.575	15.8	12.5	0.149
5	0.412	38.2	0.828	2.5	10.7	0.099
6	0.625	34.1	0.995	10.3	4	0.096
7	0.75	44.1			7.4	
8	0.694					

APPENDIX VI

Jolly-Seber estimates of the juvenile and subadult populations of small mammals present at the three study sites

Site #1, Deer Mouse population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			N.A.			N.A.
2	N.A.	N.A.	0.5	N.A.	N.A.	0.25
3	0.75	2.7	N.A.	N.A.	1.1	N.A.
4	1	N.A.	N.A.	N.A.	N.A.	N.A.
5	N.A.	N.A	N.A.	N.A.	N.A.	N.A.
6	N.A	N.A	0.4	N.A.	N.A.	0.219
7	0.375	5.3			2.1	
8	0.667					

Site #1, Meadow Vole population (meadow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			0.5			0.354
2	0.5	2	1.25	20	0.7	0.251
3	0.167	22.5	1.176	39.7	15.9	0.404
4	0.231	65	0.52	-3.5	42.4	0.147
5	0.429	30.3	1.464	3.4	8.7	0.299
6	0.643	47.8	0.677	-0.1	14.6	0.192
7	0.75	32.3			6.8	
8	0.684					

Site #2, Deer Mouse population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			N.A.			N.A.
2	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
3	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
4	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
5	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
6	N.A.	N.A.	1	N.A.	N.A.	0
7	0.5	4			1.7	
8	1					

Site #2. Red-backed Vole population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			N.A.			N.A.
2	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
3	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
4	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.
5	N.A.	N.A.	, 1	N.A.	N.A.	0
6	0.5	2	1	2.5	0	0
7	0.667	4.5			2.1	
8	0.857					

Site #2, Meadow Vole population (meadow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			N.A.			N.A.
2	N.A.	N.A.	0.6	N.A.	N.A.	0.219
3	0.5	6	1.12	4.5	3.2	0.187
4	0.5	11.2	0.843	1.4	4.9	0.189
5	0.667	10.9	1.244	2.9	2.3	0.417
6	0.778	16.4	0.407	0.2	6.2	0.179
7	0.875	6.9			2.2	
8	0.545					

Site #3, Deer Mouse population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			N.A			N.A.
2	N.A	N.A	N.A	N.A	N.A.	N.A.
3	N.A	N.A	N.A	N.A	N.A.	N.A.
4	N.A	N.A	N.A	N.A.	N.A.	N.A.
5	N.A	N.A	1.25	N.A	N.A.	1.043
6	0.5	10	0.429	10	9.9	0.324
7	0.211	14.3			3.8	
8	0.643					

Site #3, Red-backed Vole population (willow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			1			0
2	1	1	1	0	0	0
3	1	1	1	0	0	0
4	1	1	1	0	0	0
5	1	1	1	1	0	0
6	0.5	2	0.667	0.7	0	0.272
7	1	2			1.2	
8	1					

Site #3, Meadow Vole population (meadow grid)

SAMPLE	PROPORTION MARKED	POPULATION ESTIMATE	PROBABILITY OF SURVIVAL	NUMBER JOINING	STANDARD ERROR Nt(pop. estimates)	Ot(survival)
1			N.A			N.A.
2	N.A	N.A	N.A.	N.A.	N.A.	N.A.
3	N.A	N.A.	0.6	N.A.	N.A.	0.465
4	0.333	9	0.486	3.6	7.2	0.271
5	0.429	7.9	0.676	7.1	3.1	0.192
6	0.4	12.5	1.071	7.6	1.7	0.216
7	0.714	21			5.9	
8	0.556					

APPENDIX VII

Computations for the G tests regarding habitat uses

Observed and expected rate of capture of deer mice and red-backed voles in micro-habitats at site #3

	OLD GROVE WILLOW	DENSE AND INTERSPERSED WILLOW	Total
DEER MOUSE			
EXPECTED	5	14	19
OBSERVED	4	15	19
Total*	9	29	38
RED-BACKED VOLE			
EXPECTED	2	6	8
OBSERVED	4	4	8
Total**	6	10	16

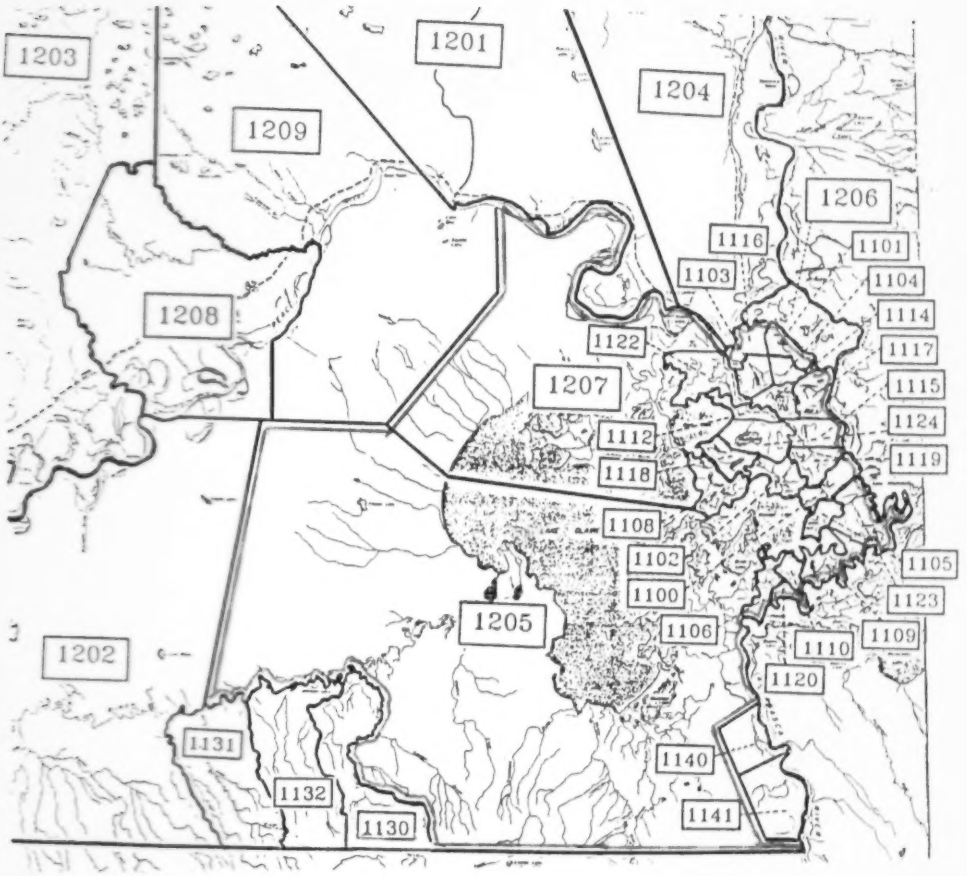
*$G_{STATISTICAL} = 0.142$ **$G_{STATISTICAL} = 1.019$

$X_{0.9[1]} = 0.016$ $X_{0.5[1]} = 0.455$

$P < 0.9$ $P < 0.5$

APPENDIX VIII

Location of the group and registered trapping areas in Wood Buffalo National Park



N.B. Trapping areas within the red boundary are considered to be within the Peace-Athabasca Delta